The Structure and Biology of Schizoneura lanigera, Hausmann or Woolly Aphis of the Apple Tree.

Part I.—The Apterous Viviparous Female.

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With Plates 38–42, and Text-figs. A–D.

I. Introduction.

The wide distribution of Schizoneura lanigera and its importance as a serious pest to fruit-growers is generally recognised by workers on economic entomology, and so far as I am aware, no detailed account of the structure of this insect has been given before. It therefore seemed to me very desirable that a study of the anatomy of this species should be carried out.

In the present paper I propose to treat of the structure of the apterous viviparous female, and hope shortly to complete the study of the winged viviparous female and other stages, which will be the subject of the second part of this paper.

I desire to take this opportunity of expressing my sincere thanks to Mr. W. F. Cooper, who has most kindly given me every facility for carrying on this work, and to Mr. L. E. Robinson for the generous and kind way in which he has given me advice during its progress.

II. Technique and Methods.

In order to ensure a constant supply of living material, several young apple-trees, both in the laboratory orchard and in the green-house, were infested with Schizoneura lanigera and kept under close observation.

For the study of the chitinous exoskeleton, entire specimens were treated with cold 10 per cent. potash for several hours, and after being washed in distilled water to which a trace of acetic acid had been added, were dehydrated, stained in xylol saturated with picric acid and mounted in Canada balsam.

Chloral hydrate and phenol in the the proportion 2 : 1 proved a useful clearing agent, the insects being left in the mixture, which was kept warm until cleared. They were then transferred direct to xylol, stained with picric acid or orange G and mounted in Canada balsam.

For the study of the head and its endoskeleton the parts were dissected out and macerated in cold 10 per cent. potash, washed, and examined in glycerine. Glycerine jelly was also used as a mounting medium.

Dissections were carried out on living and preserved material under the Zeiss binocular microscope, the specimens being fixed down on a small wax plate beneath the examination medium, special parts being isolated and examined on a slide. Normal saline solution, glycerine, 70 per cent. alcohol and oil of cloves were used as examination media. The animals resist wetting very much, which proves troublesome when dissecting living specimens under normal saline solution. If the surface of the aphid is smeared with 70 per cent. alcohol after fixing on the wax plate, and before pouring on the salt solution, the difficulty is overcome.

Entire specimens were fixed with warm picro-sulphuric acid (Kleinenberg's) formula, and Carnoy's fluid, the latter fixative giving excellent results. Internal organs were dissected out in normal saline solution and fixed with Perenyi's fluid or corrosive sublimate.

For staining sections, hæmatoxylin (Ehrlich), methylene-blue, eosin and orange G have been used. Borax carmine was used for staining organs in bulk after corrosive sublimate fixation.

Material for sections was imbedded in paraffin wax melting at 58° C., for about fifty minutes to two hours, sections being cut 6 to 10 μ thick. Material imbedded in a lower melting-point wax (45° C.) gave poor results.

The drawings have been made with the aid of the Abbé camera lucida from dissections, special preparations of parts and serial sections through the body.

III. Systematic Position, Life-History, and Habits.

Schizoneura lanigera is a member of the order Hemiptera, belonging to the family Aphididæ, the members of which are popularly known as "green fly" or "plant lice."

It is classified in the group Schizoneurini, of the sub-family Pemphiginæ.[1] On account of the quantity of white waxy threads that individuals of this species produce from the dorsal wax-glands they are known as "woolly aphis," or "American blight." This latter term is, however, misleading, as this pest, according to Theobald (1897), is European in origin, and was no doubt imported into America with imported stock. Marlatt (1897, p. 2), on the other hand, considers that the evidence is in favour of its American origin and he refers to the fact that it was first observed in England in 1787 on some stock imported from

[1] The classification of the Aphididæ is at present in an unsettled state. Passerini (1863), in his 'Aphididæ Italicæ,' includes Schizoneura under the sub-family Pemphiginæ. Buckton (1875–82) separates the Pemphiginæ and Schizoneurinæ as two distinct groups. Del Guercio (1900) classifies the genus Schizoneura in the group Myzoxylides, a division of the sub-family Myzoxylinæ. Mordwilko (1908), classifies the genus Schizoneura (Hartig, 1841), in the group Schizoneurina, a division of the sub-family Pemphiginæ. Tullgren (1909), has adopted this position for the genus in his 'Aphidologische Studien.'

America. Buckton (1880, p. 91) refers to Dr. Asa Fitch and Prof. Cyrus Thomas as refuting the idea of an American origin for woolly aphis, and also refers to Serville and Amyot as stating that it probably came to Europe through England, from America.

Owing to the transportation of nursery stock woolly aphis has been carried from one country to another, so that it is now established practically wherever the apple is cultivated.

Plant lice live on juices drawn from the tissues of growing plants, and in accordance with the sucking habits, the mouth parts, as is common amongst Hemiptera, are modified to form piercing and sucking tubes.

Schizoneura lanigera attacks practically all varieties of apple trees in Britain, producing galls on the roots and branches. It is very destructive to nursery stock and young trees. According to Theobald (1909, p. 144), who cites French (1904) and Lounsbury, apples grafted on certain stocks, particularly the Majentin and Northern Spy, do not suffer from the root form.

However, so much has been written about the habits of woolly aphis that it is, perhaps, unnecessary to say much on the point here.

Although the damage done by S. lanigera on the roots and shoots of apple trees, resulting in the formation of gall-like growths, is familiar to economic entomologists, there appears some doubt as to the exact way in which the galls are produced. Riley (1879), discussing this point with reference to Phylloxera, refers to the work of Maxime Cornu (1878), "Études sur le Phylloxera vastatrix," who accounts for the swellings caused on the vine by P. vastatrix as purely due to the piercing action of the mouth parts, and the subsequent absorption of the sap from the wounds thus formed. There are many aphids however, which, having fully developed mouth parts, do not cause galls to develop on the plant host. Some other factor must, therefore, be considered. As Riley ('Science', 1895, N.S., i, p. 457) points out in the case of the larvæ of gall-flies (Cynipidæ), it is very probable that in

S. lanigera some poisonous substance is secreted into the wound. Riley (1879) is inclined to the view that the salivary glands in Phylloxera vastatrix may produce the necessary irritating substance ; but the same argument used above may be applied in this case, for well-developed salivary glands are present in aphids which do not produce galls. Grove (1909) has described salivary glands in Siphonophora rosarum which closely correspond to those of Schizoneura lanigera, yet the former species does not produce galls on the host plant. It may be however, that the histology of the salivary glands of those species which do not produce galls differs from the species which cause galls, and that in the latter case a special ferment is produced which is not present in the non-gall-producing species.

Blomfield (1906) has described in some detail the origin and structure of the cankerous growths produced by woolly aphis. From sections through diseased galls he has shown that the effect is due to some undue influence acting on the cambium cells. He considers that the factor of mechanical irritation is not the important one, and suggests that a ferment substance is possibly produced by the salivary glands, but he failed to establish proof of this suggestion. Künckel (1867, p. 45), who inoculated plants with the extract of salivary glands of some Hemiptera, found it was innocuous.

The great damage to infected trees is caused by the fact that the soft, spongy tissue comprising the gall-like swellings gradually hardens and then cracks. These cracks enlarge owing to changing weather conditions, and thus allow the entrance of spores of the canker fungus (Nectria ditissima), as pointed out by Blomfield (1905) and Theobald (1909), and observed by the author. The question as to whether the product of the salivary glands exerts the influence on the wounds suggested by Riley and Blomfield is not at present established.

The photographs (Text-figs. A, B, C, and D) reproduced in this paper show parts of a young apple tree taken from a tree in the laboratory orchard, (i) at the end of first season of infection, (ii) during the second season after infection with S. lanigera.

A remarkable feature of aphids is the extraordinary

TEXT-FIG. A.

TEXT-FIG. B.

TEXT-FIG. A.—Schizoneura lanigera attacking branch of young apple tree (Cox's orange pippin), the second season after infection. (Photograph taken from experiment trees in the laboratory orchard.)

TEXT-FIG. B.—Schizoneura lanigera establishing itself on an injured branch of an apple tree.

numbers of young that may be produced during a season. Reproduction is largely carried on by parthenogenetic females, which give rise to numbers of living young. Throughout successive generations a series of different forms may be produced, thus resulting in a complex polymorphism. These forms may be winged viviparous females, apterous viviparous females, sexual males and females, with intermediate forms, the larvæ or "lice" and nymphs.

TEXT-FIG. C.

TEXT-FIG. D.

TEXT-FIG. C.—Schizoneura lanigera establishing itself in a wound caused by a branch being carelessly broken away from an apple tree.

TEXT-FIG. D.—Schizoneura lanigera attacking branch of young apple tree (Cox's orange pippin), three months after infection. (Photograph from experiment tree in the laboratory orchard).

As illustrating the general life-history of aphids and the relation of these different forms in the same species, it would perhaps be well to briefly describe the life-history of S. lanigera as far as is known at present.

The "mother queen"[1] may be found throughout the year on infested apple trees in crevices of the bark. It differs somewhat from the apterous viviparous female, in that the body is stouter, and of a shorter oval contour, and the legs and antennæ are shorter. She produces living young or "lice," which collect round her and form a colony.

The members of the colony secrete a number of white, waxy threads from the dermal wax glands, in which they become imbedded. The lice moult in due course and in two or three weeks become apterous viviparous females (closely resembling the queen-mother but smaller), capable of producing living young. This method of reproduction continues throughout the summer. Towards the end of summer some of the lice may develop into nymphs with a large thorax and two pairs of imperfect wings. These nymphs develop into winged viviparous females which may migrate to other apple trees and produce new colonies of living young. Reproduction goes on in this way until late in the autumn, when sexual males and females may be produced. According to Marlatt (1897, p. 3), who cites the observations of Howard and Pergande, these winged viviparous females, which appear about October or November, give rise to a "true sex generation" of lice, the females of which lay a single "winter-egg." The sexual forms of S. lanigera are rare. They are apterous, small in size, and much reduced in structure, the mouth parts being atrophied. The oviparous female lays a single egg and then dies. The fertilised eggs are laid near the base of the tree, and remaining in the cracks of the bark throughout the winter, hatch out the following spring, producing larvæ which develop into mother-queens. According to observations made by Theobald (1897), some of the adults migrate into the soil during winter and attack the superficial roots, returning to the aerial portion of the tree in spring.

[1] Buckton (1860) assigned the term "queen aphis" to the immediate issue produced from the egg which becomes the founder of a colony. German authors use the terms "Stammutter" and "Fundatrix."

IV. General Body Form (Pl. 38, figs. 1, 2, and Pl. 41, fig. 35).

The **body** of the apterous viviparous female is oval in outline. Its **colour** varies from a dull brownish-purple to a richer plum shade, the legs, antennæ, and beak being slightly paler.[1] It presents a well-marked segmentation into head, thorax and abdomen. The head of aphids, according to Huxley (1858, p. 230), consists hypothetically of six segments, but it is usually referred to as the first segment. The thorax consists of three segments, and the abdomen, theoretically, of eleven; but the terminal segments of the body are considerably reduced and only nine abdominal segments are visible. The lateral margins of the abdomen are often well developed, forming a wrinkled border or connexivum. In fully fed gravid females however, the body is much distended, the dorsum being strongly convex, and the connexivum less pronounced.

Completely covering the body is a flexible, chitinous cuticle or **integument**, which is stouter on the head and coxæ.

The **head** is strongly deflexed under the anterior end of the body, and is produced on its dorsal or anterior face as a pointed upper lip or **labrum** (*lbr.*), which lies above the mouth parts.

On its postero-ventral surface is developed the conspicuous beak or **proboscis** (*pr.*), which in repose, lies on the venter between the coxæ. It has a well-defined longitudinal groove (*l. g.*) on its anterior face, in which lie the delicate, chitinous setæ (*md.*), (*mx.*). These structures, on account of their delicate, hair-like appearance, are generally known as the "setæ."[2] In the following description I shall refer to

[1] When crushed between the fingers, a reddish blood-coloured fluid is squeezed out of the body, and hence this species is known to German authors as the Blutlaus. Sorby (1871, p. 351), who made some chemical observations on this colouring matter, calls it "aphidiene."

[2] The term "setæ" means stiff hairs or bristles, and its application to these mandibular and maxillary structures in aphids is misleading. It is however, so extensively used in the literature that I have retained it throughout this paper.

them as the **mandibular setæ** (anterior setæ), and **maxillary setæ** (posterior setæ). They are the "Stechborsten," "Russel-stilette," etc., of German authors.

The **mouth** or oral opening, which is not visible on external examination, is bounded by the oral appendages; and two lateral growths of the wall of the head form a more or less enclosed **buccal cavity** round it.

On the dorsal surface of the head is borne a pair of six-jointed **antennæ** (*a.*), behind which, situated on the sides of the head, are the **eyes** (*oc.*).

Distributed over the dorsal surface of the body are groups of **wax-secreting glands** (*w. g.*), the segmental arrangement of which is clearly indicated by the plate-like, facetted areas of the integument. These facetted integumental areas mark the position of groups of large unicellar dermal glands, which secrete the familiar masses of waxy threads. A pair of breathing pores, or **spiracles**, is situated on the ventral surface of the pro- and meta-thoracic segments (*p.s.*), (*m.s.*), but these structures are absent from the meso-thorax. There is also a pair of spiracles on the ventro-lateral surface of each of the first seven abdominal segments (*a.s.*, 1–7).

Two crescentic tubercles (*cn.*) are situated on the dorsal surface of the sixth abdominal segment. These structures represent the **cornicles** or "honey tubes" of other aphids such as **Macrosiphum**, etc.

In addition to the openings of the body described above, there are two others, the **anus** (*an.*), and the **genital orifice** (*g.o.*), situated at the posterior end of the abdomen. The former lies beneath the small, ninth abdominal segment, and ventral to it, being separated by the **anal plate** (*a.p.*), is the genital orifice.

On the ventral surface of the thoracic segments are seated the three pairs of **ambulatory appendages**, the first pair being the smallest, and the third pair the longest.

The **sense organs** consist of a pair of small eyes (*oc.*), and two sensory pits (*s. o.*) situated on the two distal joints of each antenna.

V. The External Anatomy.

The Integument.—The integument consists of two layers—an outer, chitinous cuticle, and an inner, cellular, hypodermal layer, which produces the cuticle.

The chitinous layer is thin and flexible, permitting free movement of the body segments. It is more stoutly developed on the head and legs. The hypodermis consists of a layer of epithelium, in which are scattered small, oval nuclei, but cell boundaries are not clearly defined.

Several small integumental hairs (*h.*) are distributed over the body and legs.

The Wax-secreting Glands (figs. 2 and 47).—Distributed over the dorsal integument are numerous circular or oval, facetted areas (*w. g.*) or plaques, the "Wachsdrüsenplatten" of German authors. They are arranged in transverse rows near the posterior borders of the thoracic and first seven abdominal segments, four on each segment. In addition, there are two on the eighth abdominal segment, and ten on the epicranial region of the head, the latter being situated on a thickened, quadrangular area of the cuticle, lying between the antennæ.

Each plaque consists of several polygonal areas surrounding a central facette, beneath which are situated large glandular cells. When viewed in vertical section (fig. 47), each is seen to consist of a group of large, glandular cells (*w.c.*), one cell under each polygonal facette. These cells form unicellular, dermal, wax-secreting glands, such as are found in many aphids (Pemphigus, Chermes, Lachnus, etc.), and considered by Claus (1867) to be specially modified hypodermal cells. Each of these glandular cells has a finely reticulate cytoplasm (*cy.*), and a prominent deeply staining nucleus (*n.*) situated at the free end of the cell. At the base of each cell there is an irregular lumen (*lu.*), into which the waxy secretion is poured, being passed to the exterior as waxy filaments through the chitin of the polygonal areas.

The Cornicles.—The **cornicles** (Rückenrohre of German authors, the Safthöcker of Mordwilko [1895] in Lachnus), in common with other members of the Pemphiginæ, are greatly reduced in Schizoneura lanigera. They consist of a pair of small tubercles situated on the dorsal surface of the sixth abdominal segment, near its anterior border. Each tubercle surrounds a semilunar-shaped opening, which is overhung by a lip-like thickening of the integument, its convex border being dircted towards the posterior end of the abdomen.

A section through the body in the region of the cornicles (fig. 46) shows that the integument is thickened to form a lip-like structure over the semilunar-shaped fissure (*c. o.*). Two bands of muscles (*m. cn.*) are attached to the integument near the opening of each cornicle, and passing to the ventral surface of the seventh and eighth abdominal segments, control the valve-like movements of this opening.

Lying in the posterior region of the abdomen is a delicate, wax-sac (*w. s.*), which opens at each side into the cornicles. When a living specimen is examined in normal saline solution, the wax-sac is seen to contain a pale-yellowish, oily fluid, somewhat resembling the fat-globules produced by the fat body-cells. In preserved material, however, the contents of the sac become hard, and form a conspicuous, whitish, refractive mass, which lies in the posterior end of the body. This substance is of a waxy nature, soluble in xylol, but insoluble in alcohol, water, and glycerine. In sections mounted after treatment with xylol, the delicate wall of the wax-sac is seen surrounding the empty cavity of the sac, whose contents have been dissolved by the xylol.

The question as to the function of the cornicles in aphids has occupied the attention of many observers. It would appear from the literature that the term "honey-tubes," which is often applied to these structures, is a misnomer.

According to the resumé of the subject given by Horvath (1904), Réaumur (1737), one of the earlier observers, thought that these structures had an excretory function. Bonnet

(1745), was of the opinion that they excreted a sweet fluid and were concerned with the respiratory and excretory system, this view being adopted by Kyber (1815), Morren (1836) and Kaltenbach (1843). Linné (1758) expressed the opinion that a honey substance was secreted from the cornicles, and this view was fairly generally adopted. Of more recent authors, Witlaczil (1882) considered that sugary substances were excreted from the cornicles. Büsgen (1891), referring to analyses made by Knorr on the secretion produced from the cornicles, showed that it must be regarded as a waxy substance. Mordwilko (1995, p. 363) has demonstrated the waxy nature of the substance underlying the cornicles in Lachnus viminalis. Horvath (1904), in his paper, "Sur les cornicles on nectaires des Aphidiens," concludes, as the results of observations made, that the cornicles are secretory canals from wax-producing glands, specially differentiated, the product of which is a waxy fluid, which affords a means of protection against the predaceous larvæ of Coccinellidæ and Chrysopidæ. According to this author the honey substance which attracts ants is produced in clear droplets from the anus. Some American authors (Gillette, 1908), have confirmed Horvath's observations. The author has frequently observed in S. lanigera large clear and transparent drops emerging from the anus, which were quite colourless. Buckton (1875, p. 47), has described similar drops in the case of Schizoneura ulmi. (See also Mordwilko, 'Biol. Centrlb.,' xxvii, 1907, pp. 212 et. seq.)

The Head and its Appendages (figs. 1, 3, 22–24, 35).—The **head** is borne at the anterior end of the body, and bears the oral appendages which surround the mouth. At its proximal end it broadens out to become continuous with the prothorax. Towards its distal end it becomes narrower, and is strongly deflexed. It is divided by a pseudo-articulation of membranous chitin (*a. f.*) into a broad, proximal portion, the **epicranium**, which bears the small eyes and the antennæ; and an anterior tapering portion (*fr.*), which includes the **clypeus** and **labrum**. This anterior portion is composed of stout chitin, and is strongly dome-shaped on its anterior face. It freely articulates with the epicranium by means of thin, flexible chitin (figs. 23, 24), and is continued above the mouth as the pointed **labrum** or upper lip (*lbr.*). It has been termed the "frons" by some American writers (Ashmead, 1889, p. 185), and is the "Vorderkopf" of German authors. Bugnion (1911, p. 649) recognises the homology of this structure in Hemiptera with the clypeus of other insects. A slight transverse ridge occurs at the junction of the clypeus and labrum.

The appendages of the head consist of the antennæ and the buccal appendages, the latter comprising the labrum, a pair of mandibles, the maxillæ, and the proboscis or beak (second maxillæ).

The **buccal appendages** of aphids are now generally accepted as homologous with the mouth parts of other insects as follows: the proboscis represents the labium, its anterior wall being continued beneath the mouth as a small underlip or hypopharynx; the anterior pair of setæ the mandibles; the posterior pair of setæ the maxillæ ii, the labrum being distinct as a triangular prolongation of the clypeus. Smith (1892, p. 189) considers the setæ represent the lacinia and stipes of the maxillæ, developed as in the Diptera. This conception of the buccal appendages of Hemiptera was, however, proved to be erroneous by Marlatt (1895, p. 241), but Smith states in a later paper (1898, p. 176) that he is still of the opinion that the proboscis and setæ are maxillary structures, and that no trace of mandibular structures occur in any present Hemipterous form. Marlatt (1895, pp. 241–249), as a result of careful investigations on the structure of the mouth parts of Cicada, shows that the mandibles in this insect are represented by two small sclerites and the anterior setæ, to which the swollen bases of the latter structures are attached. Similarly the maxillæ are represented by two narrower sclerites, to which the posterior setæ are attached. In the lower families of Hemiptera Marlatt states that these sclerites are minute or obsolete.

Smith (1892) observed the presence of these sclerites in Hemiptera, and Marlatt remarks that prior to this author's work the mandibles and maxillæ were supposed to be represented by the setæ alone.

Marlatt (1895, p. 247) states in error that the mandibular setæ in aphids become intimately united ; it is the posterior pair of setæ (the maxillæ) which fuse, and not the mandibular setæ.

Bugnion (1911, p. 643), who cites Heymons (1896–8), "Die Mundtheile der Rhynchota," 'Entom. Nachr. Jahrg.,' xxii, No. 11, p. 173), points out that this author showed that the setæ in Hemiptera only represent part of the mandibles and maxillæ, the other portions of these structures being more or less fused with the wall of the head.

I have not observed any chitinous sclerites attached to the setæ and extending from the wall of the head, except those mentioned above as the mandibular and maxillary chitinous rods. These are evidently supporting structures for the setæ. The basal portion of each seta is not in any other way connected with the wall of the head. The insertion of the protractor muscles on the mandibular rods would seem to show that these rods are part of the mandibles.

The proboscis is now generally accepted as being homologous with the labium of other insects.

As regards the function of the buccal appendages, the proboscis acts as a supporting structure for the setæ and is not used as a piercing organ. Marlatt (1895) has made observations verifying this point. The close fusion of the maxillary setæ in the proboscis groove forms a fine canal along which the plant juices are drawn.

The relationship of the buccal appendages will be best understood from the series of sections through the head and anterior part of the body, shown in figs. 6–12, 23–24, 25–31.

The **labrum** is the anterior prolongation of the clypeus. It tapers towards its free end, and is slightly grooved on its posterior or internal face, the chitin of the external face being marked with a few minute, transverse ridges.

The **proboscis** (*pr.*) is formed by an evagination of the integument at the infra-posterior end of the head. It may be withdrawn into the body for some distance, somewhat after the manner of an inverted glove finger, the integument forming a sheath round it, as shown in fig. 34. I have seen specimens with about a half of the beak retracted. It consists of three segments—a long proximal segment, a short middle segment, and a tapering distal segment, at the extremity of which are a few sensory hairs (*s. h.*). A well-defined **longitudinal proboscis groove** (*l. g.*), in which lie the mandibles and maxillæ, runs along the length of its anterior face.

Situated beneath the mouth is the small **hypopharynx** (*h.*) which supports the chitinous salivary pump (*s.*) and is continuous with the labium (proboscis).

The **mandibles** (*md.*) consist of a pair of delicate, chitinous structures which emerge from the head, at the side of the mouth, and extend along the proboscis groove. They are finely pointed at the distal end.

At their proximal ends, which are situated in the head, they are greatly enlarged, and each is attached to a stout **mandibular chitinous rod** (*m .r.*).

The **maxillæ** (*mx.*) consist of two similar structures, being situated immediately posterior to the mandibles, but before leaving the head to enter the buccal cavity, they fuse to form a single seta, which lies between the mandibles in the proboscis groove.

An elongate **maxillary chitinous rod** extends from the wall of the clypeus beneath each maxilla with which they fuse.

At the sides of the mouth the lateral walls of the clypeus are produced downwards as two-lobed structures, which partly enclose the buccal cavity. This is shown in the series of transverse sections through the head (figs. 6–12). It will thus be seen that the labrum, labium, and these lateral lobes of the head form a more or less enclosed **buccal cavity** (*b. c.*) surrounding the mouth.

I shall discuss the oral appendages in greater detail when describing the digestive system.

The **antennæ** (fig. 4) are composed of six articles, of which the third article is conspicuously longer than the others. The two proximal articles are about equal in length, the basal one being slightly broader. The third article is cylindrical in shape, and almost as long as the three distal articles together. The fourth and fifth articles are slightly broader distally, and the terminal one attenuates abruptly at the distal end, forming a short, blunt process, which bears a few sensory hairs. Each of the two distal articles bears a sense organ (*s. o.*), which consists of a circular pit, surrounded by a ring of sensory hairs. A few hairs are scattered over the surface of the articles.

There are no compound eyes such as are found in the winged viviparous stage. Two **small eyes**, each consisting of three **tubercles**, are borne behind the antennæ, one on each side of the head. As seen in section (fig. 49), they consist externally of three transparent convex **tubercles**, beneath which are grouped, in close contact, three densely pigmented areas (*om.*) These areas are somewhat pear-shaped, the long axes being at right angles to the surface of the head, and the tapering portion internal. A delicate strand of nerve-fibres (*oc. n.*) passes from each eye towards the brain. The apterous viviparous female is sluggish in habits, living in the dark cracks of galls or imbedded amongst the members of the colony, which accounts for the poorly developed eyes.

The Thorax and Ambulatory Appendages.—Each of the thoracic segments bears on its dorsal surface four groups of **wax-secreting glands**, and on its ventral surface a pair of legs. Situated on the ventral surface of the prothorax, near its posterior border, are the two **pro-thoracic spiracles** (*p. s.*). Two **meta-thoracic spiracles** (*m. s.*) are situated near the anterior border of the meta-thorax.

The **legs** are composed of five articles—a small basal article or coxa (*cox.*), a short cylindrical trochanter (*tro.*), the femur (*fe.*), tibia (*ti.*) and tarsus (*ta.*).

The **femur** is elongate and slightly broader distally. The **tibia** is elongate and of uniform thickness. The distal article or **tarsus** consists of a small basal joint (*b. ta.*) and a longer, slightly curved, distal joint, which bears a pair of curved claws (*cl.*) and a few tactile hairs.

The anterior pair of legs is the shortest, the mesothoracic legs being slightly longer, and the third pair the longest. A few hairs are borne on each of the articles.

The Abdomen.—The **abdomen** consists of nine visible segments.[1] The terminal or ninth segment (*abd.* ix) is very small, and is not prolonged into a cauda or tail, such as is found in many aphids. Situated below the terminal segment, opening on the dorsal surface of the body, is the **anus** (*an.*), immediately beneath which is the conspicuous **anal plate** (*a. p.*). This latter structure is an arched, lobe-like development of the integument, which extends beneath the anus and the genital orifice, and bears numerous stout hairs.

The transverse **genital orifice** (*g. o.*) is situated ventral to the anus, being overhung by the anal plate. On the ventral border of this opening the integument is developed to form a small semilunar-shaped **genital plate** (*g. p.*), which bears stout hairs.

The **abdominal spiracles** are situated on the ventral surface, near the lateral margins of the body, in the wrinkled membranous chitin at the anterior borders of the first seven segments.

[1] The number of segments in the abdomen of aphids is a disputed point, owing to the modification of the terminal segments. Balbiani (1869, p. 64) refers to the work of Lacaze-Duthiers (1853), 'Recherches sur l'armure genitale femelle des Insectes,' who considers that the typical number in insects is eleven. According to Buckton (1875, p. 20), this latter author has shown that in most Hemiptera there are three segments intervening between the genital orifice and the anus, and as Balbiani observes, the absence of the terminal segment in aphids must be attributed to the atrophy of one of the post-genital segments. Kaltenbach (1843) considers there are only nine segments. Tullgren (1909) considers there are only nine visible in Schizoneura, and I have adopted his terminology.

VI. The Internal Anatomy.

The internal anatomy of Schizoneura lanigera, so far as I am aware, has not been studied in any detail before. Indeed, considering the great economic importance of the Aphididæ, our knowledge of the anatomy of this family is very small. Several of the earlier workers on aphids, such as Dufour (1833), Morren (1836), Kaltenbach (1843) and Buckton (1875–82), treated in a general way of the anatomy of the group. Later, Balbiani (1866, etc.), Mark (1877), Witlaczil (1882, 1884), and Will (1888), have done much to further our knowledge of the internal structure and histology of these important insects. Of more recent contributions to the literature of aphid anatomy, the works of Dreyfus (1889 and 1884), Krassilstschik (1892–3) on Phylloxera vastatrix, Mordwilko (1895) on the anatomy of Trama and Lachnus, Flögel (1904) on Aphis ribis and Grove (1909) on Siphonophora rosarum may be cited.

Distribution of the Internal Organs.

When the dorsal integument is carefully removed under normal salt solution from a living, apterous viviparous female of S. lanigera, as shown in fig. 5, numerous olive-coloured **fat body cells** are seen, lying beneath which are a number of oval yellowish-brown **embryos** (*e.*), in various stages of development. These embryos are contained in long, thin-walled tubes or the **ovarian cæca** (*p. c.*), which are transversely constricted along their length to form several large **ovarian chambers**, in which the embryos are borne. The cæca are arranged in two groups, one group on each side of the median line, with about four or five cæca in each, and extend throughout the greater part of the body. In the posterior region of the abdomen the tubes from each side lead into a wide **oviduct** (*od.*), and the two oviducts enter into a median, muscular chamber, the **vagina** (*v.*), which leads to the **genital orifice.**

On removing the embryos from the dorsal surface the whitish-yellow coils of the digestive canal are seen lying beneath.

The **alimentary canal**, as seen in side view (fig. 35), leads from the **mouth** into a well-defined **pharynx** (*ph.*), which structure passes upwards through the head, and leads into the narrow, tubular œsophagus (*œs.*). The **œsophagus** passes in the median line over the thoracic ganglion (*t. g.*), and enters into the stomach (*st.*) or sac-like dilation of the mid-gut. The **stomach** narrows towards its posterior end, and leads into the coiled **intestine** (*i.*), from which the **rectum** (*r.*) passes in the median line over the vagina (*v.*) to the **anus** (*an.*).

The **salivary glands** lie obliquely in the thorax, above the œsophagus, and consist of a small anterior gland (*s. a.*) and a large posterior gland (*s. p.*), situated on each side of the median line. The salivary duct from each side passes beneath the thoracic ganglia, and both unite in the mid-ventral line to form a median salivary duct (*s. d.*) which leads to the **salivary pump** (*s.*), situated at the posterior end of the buccal cavity.

The **supra-œsophageal ganglia** occupy the greater portion of the head. Extending beneath the œsophagus is an elongate ganglionic mass, which comprises the sub-œsophageal ganglion, with its two broad commissures, and the fused thoracic and abdominal ganglia.

The **respiratory organs** consist of fine tracheal tubes, which ramify over the body in two definite systems, a dorsal and a ventral tracheal system, the main tracheæ from which lead on each side of the body to the nine pairs of spiracles.

Four conspicuous bands of **longitudinal muscles** extend along the floor of the body, two on each side of the median line, and four similar bands extend beneath the dorsal segment.

A. The Digestive System (Pl. 38, fig. 5; Pl. 41, fig. 35).

The **mouth** or oral opening is situated on the ventral surface of the head, being bounded anteriorly by the labrum (*lbr.*), and posteriorly by the hypopharynx (*h.*) and proboscis (*pr.*). Laterally it is bounded by the lateral lobes of the clypeus, mandibles (*md.*), and the maxillæ (*mx.*), and leads into the suction canal formed by the fusion of the maxillæ.

The Pharynx.—The mouth leads upwards into the pharynx. This structure is a distensible chamber lined with chitin, which is continuous with the cuticle of the body. Its posterior or ventral wall is strengthened by a stout layer of chitin, but its anterior wall is composed of flexible membranous chitin. As seen in transverse sections (figs. 12–20) the pharynx is crescentic in shape, its greatest transverse diameter being near the oral end. Its walls in this region are thickened to form two hollow, dome-shaped protuberances (*p. p.*) or ridges, the "Naröiden" of Dreyfus (1894) in Phylloxera. The lumen of the pharynx in this region is very narrow, and divaricator muscles (*m. ph.*) pass from its dorsal wall to the wall of the clypeus. Two folds of chitin extend from the clypeus to the wall of the pharynx protuberances, with which they fuse.

The pharynx is well supplied with muscles. Attached to its anterior flexible wall are several bands of divaricator muscles, which extend to the anterior wall of the clypeus. These muscles are divided into fine tendons at their attachment on the chitinous walls of the clypeus. By means of these muscles, the anterior wall of the pharynx is drawn outwards and the lumen of that structure is greatly enlarged, the plant juices being drawn into it through the mouth. I have pointed out that the lumen in the region of the pharynx protuberances is very narrow, and ventrally has stout chitinous walls. When the divaricator muscles of this region are relaxed, the entrance into the pharynx chamber is almost closed, preventing the plant juices from returning into the mouth. As the other divaricator muscles of the pharynx are relaxed, the anterior wall of that structure, on account of its flexibility, tends to regain its original shape, and the cavity, being thus greatly reduced in size, the juices are forced backwards into the œsophagus.

The Endoskeleton of the Head (Pl. 38, fig. 3; Pl. 39, figs. 6–24; Pl. 40, figs. 25–32).—The **chitinous endoskeleton** of the head consists of an arrangement of chitinous rods or endosternites, which, in addition to giving support to the head, afford attachment for muscles of the head and its appendages. The endoskeleton in S. lanigera agrees closely with that described by Dreyfus (1894) in Phylloxera and Mordwilko (1895) in Lachnus.

Situated in the posterior portion of the head, beneath the supra-œsophageal ganglion, is a hollow, chitinous plate or bar (*t.*), which forms the central support of the endoskeleton. This structure corresponds to the "Chitinstab" of Mordwilko (1895) in Lachnus, named after Witlaczil (1882). It is also the "arcus superior" of Mark (1877), Krassilstschik (1892–3), and other authors. Grove (1909) suggested the term "**transverse bar**" for the corresponding structure in Siphonophora rosarum, and throughout my description of S. lanigera I shall use this term.

Four hollow rods of chitin are fused with the transverse bar and pass from it to the walls of the head. They are as follows:

A pair of **antero-dorsal rods** (*a. d.*) (the Arcus inferiores) of Mark (1877), Dreyfus (1894) and Mordwilko (1895), pass dorsally, one from each end of the transverse bar in an antero-lateral direction to the roof of the head, joining it at the junction of the clypeus and epicranium. From here a ridge of chitin (costæ inferiores of Mark, Dreyfus, etc.) passes on each side of the clypeus along its lateral walls, with which they fuse.

A pair of **antero-ventral rods** (*a. v.*) embracing the arcus superiores and costæ superiores of Dreyfus and Mordwilko pass ventrally from the ends of the transverse bar, in an antero-lateral direction, towards the infra-posterior border of the head, each being then reflected along the lateral walls of the clypeus to a position opposite the swollen proximal ends of the mandibles, where they fuse with the wall of the head. From this region, on each side, a stout chitinous rod passes at right angles into the head towards the proximal end of each mandibular seta. A narrower and more elongate rod passes beneath each maxillary seta. These structures I have called the mandibular (*m. r.*) and maxillary (*mx. r.*) chitinous rods.

The **mandibular rods** are stouter than the maxillary rods, and expanding at the base, fuse with the continuation of the antero-ventral rods and the antero-lateral walls of the clypeus.

The **maxillary rods** are attached at the base of the mandibular rods, from whence they curve ventrally, pass beneath the proximal portion of the maxillary setæ and fuse with them.

Two thin rods of chitin (*v. r.*) ("Chitinfortsatzestabchen" of Mordwilko), to which are attached a few muscles from the salivary pump, arise from the posterior end of the buccal cavity and extend beneath the pharynx towards the transverse bar where they fuse.

The Buccal Appendages.—The **buccal appendages** consist of the **labrum**, **mandibles**, first pair of **maxillæ**, and the proboscis or **labium**.

The labrum and labium have been described above under the head appendages.

The mandibular setæ (*m. r.*) are situated in the head below the pharynx, being supported by the two mandibular chitinous rods described above. At their proximal ends they are greatly enlarged, but as they pass towards the buccal cavity they become considerably attenuated and approximate closely to one another in the median line. They are finely pointed at their distal ends, and each is composed of stout chitin with an extremely fine cavity running throughout its length. After leaving the head they pass through the buccal cavity and extend along the proboscis groove. The flexible chitin of the buccal cavity is attached to the walls of the mandibles, which thus permits of free movement of these structures (fig. 33). When they are retracted into the head, the sheath is drawn inwards after the manner of an inverted finger of a glove.

The maxillary setæ (*mx. r.*) are situated immediately posterior to the mandibles, which they resemble in structure.

As they enter the buccal cavity they fuse to form a single chitinous seta, which extends between the mandibles along the proboscis groove and encloses two minute canals.

Inserted on the internal face, at the proximal end of each of the mandibular setæ, is a strong **mandibular retractor muscle** (*m′. m.*), both of which extend in a postero-dorsal direction to become attached respectively to the right and left antero-dorsal rods of the endoskeleton, near the ends of the transverse bar. A similar **maxillary retractor muscle** is attached to each of the maxillary setæ (*m′. mx.*), and extend to the post-ventral rods, being attached to them near the ends of the transverse bar.

The Retort-shaped Organs.—Extending from the proximal end of each of the setæ is an elongate, compact mass of small cells possessing well-stained nuclei. They are shown in fig. 22 (*md. o.*), (*mx. o.*). These structures are related to the peculiar, **retort-shaped organs** (*re. o.*) found lying in the thorax and posterior part of the head in well-developed embryos of S. lanigera and other aphids. In advanced embryonic stages they are large and conspicuous, being of a characteristic retort shape. From the neck of each retort a long, fine, chitinous tube, the so-called "seta," is produced, which may frequently be seen coiled round these organs in the anterior part of the embryo.

These retort-shaped structures are bounded externally by a chitinous membrane and an epithelial layer of cells, with elongate, flattened nuclei; and the interior of the retort is packed with a mass of small cells possessing deeply staining nuclei. As development proceeds from the larval stage to the adult they appear to degenerate, so that in the adult apterous viviparous female, after completion of the moultings, they are sometimes difficult to make out. Krassilstschik (1893, p. 9) says that in fully developed adults of Phylloxera vastatrix the retorts completely disappear. I have observed them in all the longitudinal sections of the apterous viviparous females of S. lanigera examined, although they usually appeared to be in a degenerate condition.

Mecznikow (1866, p. 462) states that during the development of Aphididæ, the structure in the early embryonic stages corresponding with rudimentary mandibles and maxillæ disappear, and that the retort-shaped organs found in more advanced embryos become elongated at the neck end and produce the "Russelstilette," and Mayer (1875, p. 335), in describing the origin of the "Stechborsten" in Pyrrochoris apterus, states that the retort-shaped organs observed throughout the development of this insect, are to be considered as the "Bildungstatten" of those structures. Witlaczil (1882, p. 415) is of the opinion, that the embryonic "Anlagen" of the mandibles and maxillæ do not disappear, but sink into the head, and give rise to the retort-shaped organs.

I propose to discuss the question as to the structure of these organs and their relation to the mandibles and maxillæ in greater detail when dealing with the anatomy of the larva.

The Salivary Glands.—The **salivary glands** are whitish glandular bodies, situated in the prothorax and posterior region of the head. They consist of two pairs[1] of glands, which lie above the thoracic ganglion, one pair on each side of the œsophagus. Each pair comprises a large posterior gland and a smaller anterior gland.

The **posterior salivary gland** (*s. p.*) is large, oval in shape, and lies obliquely in the prothorax.

The **anterior salivary gland** (*s. a.*) is small, spherical in outline, and situated close to the anterior end of the posterior gland.

A narrow duct leads from the anterior end of each posterior gland, near to which it receives a small duct from the anterior gland. The **salivary duct** from each side passes

[1] In some Aphids three glandular bodies have been described, as in Phylloxera vastatrix (Krass, 1893); also in Aphis ribis (Flögel, 1905). In these cases, as Mordwilko (1895) points out, the large posterior gland described above, may be bi-lobed. The small anterior gland, on account of its small size, was overlooked by some of the earlier workers. Mark (1877) has figured the salivary glands of S. ulmi, which correspond closely to those in S. lanigera.

in an antero-ventral direction beneath the thoracic ganglion, and both unite in the mid-ventral line to form a bulbous expansion in the infra-posterior region of the head. From here the salivary duct (*s. d.*) continues beneath the large pump muscle (*m.*) as a single median duct, and decreasing considerably in size, leads into the **salivary pump** (*s.*), which is situated in the hypopharynx at the posterior end of the buccal cavity.

The salivary glands are simple in structure (fig. 41). The posterior gland is a sac-like body consisting of an epithelial layer of large, conical cells, which bulge into the irregular cavity (*lu.*) of the sac. These cells possess fine, granular cytoplasm (*cy.*) and prominent, deeply staining nuclei, and border on the irregular lumen of the gland, which leads at the proximal end, by a narrow channel, into the salivary duct. The cells in the posterior portion of the gland appear to be filled with secretion, the nuclei are larger, and the cell contents appear less granular than in the anterior portion.

The cell boundaries of the anterior glands are not well defined, and the lumen is almost entirely reduced. A few large, deeply staining nuclei are present, imbedded in a granular cytoplasm.

The walls of the salivary duct are comparatively thick, and enclose an extremely fine lumen, along which the salivary secretion is passed. Several nuclei are seen in the walls, but cell boundaries are not well defined.

The Salivary Pump.—Lying beneath the anterior end of the pharynx, being supported by the small hypopharynx, is the **salivary pump** (*s.*) or "Speichelpumpe" of German authors, into which the salivary duct conveys the products of the salivary glands, which then pass along a fine canal in the fused maxillæ. This structure corresponds in position to the "Wanzenspritze" described by Wedde (1885) in the Rhynchota. It has been observed by Mayer (1873) in Pyrrhocoris, Mark (1877) in Chionaspis, Witlaczil (1882) in Aphids and Coccidæ, Dreyfus (1894) in Phylloxera, and other authors. Krassilstschik (1892–93) has described its structure in Phylloxera vastatrix. Kershaw (1911) has recently described the structure of the pump in Pristhesancus papuensis, a species in which this organ is well developed. My observations on the salivary pump agree closely with those of Dreyfus (1894) in Phylloxera vastatrix.

When seen in longitudinal section (fig. 24), the salivary pump in Schizoneura lanigera consists of a **salivary chamber** (*s.c.*) or "Kolben," whose outer walls form the **cylinder** (*cd.*) and a strong, distal portion or shaft, which is strongly chitinised and laterally compressed, its chitinous walls being continuous with that of the hypopharynx.

At its closed proximal end, as will be seen in vertical sections through the head (figs. 31, 33), the cylinder is greatly enlarged, its outer walls being strongly chitinised. Its posterior wall is membranous, and invaginated into the cylinder, thus forming a space, the salivary chamber, between this wall and the outer walls of the cylinder. On this posterior concave wall is inserted the large **pump muscle** (*m.*), which extending beneath the pharynx, becomes attached to the transverse bar of the endoskeleton.

The salivary duct leads beneath the pump, and apparently enters into the salivary chamber on its ventral surface, but I have not been able to definitely trace its entry into the chamber. Kershaw (1911) describes and figures in Pristhesancus papuensis a valvular entrance from the salivary duct into the cylinder, or what this author terms the "syringe barrel," but I have not observed this in Schizoneura lanigera.

The working of the pump is largely controlled by the large pump muscle (*m.*). When this muscle contracts, the invaginated posterior wall of the cylinder is pulled outwards, and the cavity of the salivary chamber being enlarged, the contents of the salivary ducts are drawn into it. When the muscle is relaxed, the posterior wall of the cylinder, which is membranous and elastic, tends to regain its original position, and the lumen of the cavity being thus reduced, the saliva is forced along the pump shaft into a fine canal down the fused maxillæ.

The Œsophagus.—The **œsophagus** (*œs.*) leads as a narrow, straight tube from the posterior end of the pharynx, and passing through the circum-œsophageal ring, over the transverse bar, extends in the median line above the thoracic ganglia.

In the mesothorax it enters into the stomach or dilated region of the mid-gut.[1] When examined as a fresh preparation in normal salt solution, it appears as a whitish-grey, semi-transparent tube, with comparatively thick walls, which surround a very small lumen.

The **walls of the œsophagus** consist of an epithelial layer composed of granular protoplasm, in which are scattered small, elongate nuclei, but cell boundaries are not well defined. A thin, outer coat of connective tissue surrounds the epithelium.

The mid-gut.—The **mid-gut** extends somewhat obliquely in the median line, its anterior portion being considerably enlarged to form the stomach, which is the widest part of the alimentary canal. As will be seen in longitudinal sections, the œsophagus is invaginated for some distance into the stomach, its walls being reflected back to become continuous with the walls of that structure, thus forming an effective **œsophageal**

[1] This expanded portion of the digestive tract in aphids is sometimes referred to as the "crop." The crop in insects is associated with the stomodæum, being derived from ectoderm, and lined with a chitinous intima. The cells composing the wall of the expanded portion of the mid-gut in S. lanigera agree in character with those in other parts of the wall of the mid-gut. Further, the place where the oesophagus terminates and the large cells of the expanded portion of the gut commence is clearly defined. There is no chitinous intima in this region. Of course, the absence of a chitinous intima is not in itself proof of its mesodermal origin, as a chitinous lining is found in the mid-gut of many insects, as shown by Schneider, but in these cases its origin is doubtful. This structure must be considered as part of the mid-gut, and the term "crop" is erroneous. I shall refer to this portion of the gut embracing the œsophageal valve as the stomach. It is the "Magen" of Dreyfus (1894) and others.

valve (fig. 48), which prevents the regurgitation of plant juices from the mid-gut to the œsophagus.

A band of **connective tissue** (*c. t.*) extends from the œsophagus across the shoulder of the œsophageal valve, forming a kind of ligament which is continuous with the connective-tissue coat of the œsophagus and stomach.

The **stomach** forms a thick-walled sac with a wide lumen, which is usually filled with plant juices. Its wall consists of an epithelial layer of large, conical cells, the free ends of which bulge into the cavity of the sac (fig. 40). Externally there is a thin layer of connective-tissue. Towards the posterior end of the stomach the lumen decreases in size, and the cells become flatter.

At the base of each cell is a prominent deeply-staining nucleus, which is embedded in a mass of granular secretion. The granules are also densely crowded throughout the cytoplasm. It is probable that these cells function as digestive glands, and pour digestive secretions into the lumen of the stomach. Along the free end of the cells there is a well-defined margin, which, bordering the lumen, stains deeply with eosin.

At its posterior end the stomach narrows considerably, and becomes continuous with the **coiled intestine.** The structure of the walls of the latter closely resembles that of the stomach, but the cells are not so conical, and the granular elements in the cytoplasm not so dense. The lumen of the intestine is greatly reduced, and usually tri-radiate or irregular in section.

When seen in fresh preparations the mid-gut is whitish-grey in colour, semi-transparent, with the large nuclei of the epithelial cells showing conspicuously through the walls. The general course taken by the intestine may be described as follows (figs. 5 and 35).

The stomach extends obliquely in the median line to about the third or fourth abdominal segment, where it leads into the intestine (*i.*), which turns abruptly on itself in an antero-ventral direction. In the posterior half of the thorax the intestine increases in size, and lies transversely across the median line above the anterior end of the stomach, turning abruptly on the left of the median line in a posterior direction beneath that structure. About the third abdominal segment it narrows considerably, and passes beneath the stomach towards the thorax, where it again bends at right angles across the median line, and leads into the rectum (*r.*), which continues in a postero-median direction towards the anus.

The coils of the alimentary canal lie beneath the large ovarian cæca, near the ventral surface of the body, and are held in position by strands of connective tissue and fine ramifying tracheæ.

The Rectum.—The **rectum** or posterior chamber of the hind-gut continues in a post-median direction as a thin-walled tube, and passing between the two oviducts, extends upwards above the vagina to the anus. In some individuals it is distended in a sac-like manner, but attenuates towards the anus.

The structure of the wall of the rectum (fig. 37) differs from that of the mid-gut. It is composed of an irregular epithelium which bounds the lumen. The cell walls are not clearly defined, but conspicuous nuclei are embedded throughout the epithelium. A delicate, chitinous intima, continuous with the body integument, extends for some distance along the rectum.

Two bands of divaricator muscles are attached to the rectum near the anus, and pass to the body-wall.

Malpighian tubes are absent in S. lanigera. Kowalevsky (1889), as cited by Mordwilko (1895, p. 353) and other authors, has shown that in insects which have no Malpighian tubules, the cells of the rectum wall may have an excretory function.

B. The Nervous System (figs. 35 and 36).

The **nervous system** is concentrated in the head and thorax. It consists of a pair of fused **supra-œsophageal ganglia** (*s. g.*), which occupy the greater part of the head; a pair of fused **sub-œsophageal ganglia**; and an elongate **median ganglion**, lying in the thorax beneath the œsophagus. The latter represents the fused elements of the ventral nerve chain, and comprises the three fused **thoracic ganglia**, to which the sub-œsophageal ganglia are attached by two broad commissures, and a **median abdominal ganglion.** Nerves are given off from the ganglia to the appendages and other parts of the body.

The **supra-œsophageal ganglia** occupy the epicranial region of the head. They consist of two fused, pear-shaped ganglia, which have their widest part towards the anterior or dorsal wall of the head (figs. 18, 21). Histologically they consist of an outer coat of ganglionic cells with deeply staining nuclei, and an inner, lightly stained area composed of an interlacing mass of nerve fibres.

Near the infra-posterior end of these ganglia, two short **circum-œsophageal commissures** (*cs.*) lead round the œsophagus, and connect with the sub-œsophageal ganglion, forming a loop through which the œsophagus passes.

From the antero-dorsal end of the supra-œsophageal ganglia a pair of antennal nerves (*n. a.* fig. 21) are given off laterally to the antennæ, behind which are a pair of small nerves which pass to the eyes.

The sub-œsophageal ganglion (*sb. g.*) is smaller, and is connected with the thoracic ganglia by means of two broad commissures. From its anterior end a pair of small nerves arise, which innervate the proboscis, and another pair innervate the maxillæ and mandibles.

The fused **thoracic ganglia**, together with the **median abdominal ganglion** (*a. g.*), form an ovoid, elongate mass, which extends in the median line along the ventral surface of the thorax.

The histological structure of these ganglia is the same as before, consisting of an outer coat of ganglionic cells possessing nuclei of varying sizes, and an inner, whitish-grey, medullary region, composed of an interlacing network of nerve-fibres.

From each of the thoracic ganglia a pair of nerves is given off laterally, which pass into the legs ($n.\ l_1.$–$n.\ l_3.$). These nerves bifurcate before entering the coxæ. From the posterior end of the abdominal ganglion a stout **post-abdominal nerve** (*p.*) extends in the median line beneath the alimentary canal, almost to the posterior end of the body. At its extremity, beneath the vagina, it expands into an irregular club-shaped **post-abdominal ganglion** (*p. g.*), from which nerves pass to innervate the vagina and muscles of the terminal abdominal segments. Several nerves are given off along the length of the post-abdominal nerve. They arise more or less irregularly in pairs, and pass in a post-lateral direction to the abdominal segments, especially innervating the longitudinal bands of muscles on the floor of the body.

c. The Respiratory System (Pl. 38, fig. 5; Pl. 41, fig. 39).

The **respiratory system** consists of a dorsal and ventral system of tracheal tubes, the main trunks from which communicate with the exterior by means of nine pairs of spiracles. Each spiracle consists of a small opening surrounded by a chitinous ring. Each of the first seven abdominal segments bears a pair of spiracles, which are situated on the ventral surface, near the lateral margins of the body.

The two **pro-thoracic spiracles** are situated external to the coxæ on the ventral surface of the prothorax, near its posterior margin. Two similar **meta-thoracic spiracles** (*m. s.*) are situated near the anterior border of the metathorax. There are no spiracles on the mesothorax.

Dorsal Tracheal System.—Leading from each spiracle is a short tracheal trunk (*s. r.*), which bifurcates into a dorsal (*d. b.*) and a ventral (*v. b.*) tracheal branch. The dorsal branches from the spiracles pass upwards, more or less parallel to one another, along the lateral walls of the body to the dorsal surface, and then inwards towards the dorso-median line. At some distance from the median line the dorsal branches from all except the prothoracic spiracles bifurcate, and join to form on each side of it a main **dorsal longitudinal trachea** (*d. t.*), which extends beneath the dorsal integument in a zig-zag longitudinal course, from the prothoracic to the seventh abdominal spiracle.

One of the divisions of the dorsal branch from each of the seventh abdominal spiracles passes inwards, and both fuse in the median line, thus connecting the two lateral divisions of the dorsal tracheal system.

Several small bunches of tracheæ, which ramify over the reproductive organs and alimentary canal and aerate the dorsal longitudinal muscles, are given off from the dorsal longitudinal trachea.

From the prothoracic spiracles a stout trachea (*a. t.*) passes anteriorly, and branching considerably, aerates the cephalic ganglia and muscles of the head, a branch passing to the antennæ.

Ventral Tracheal System. — The ventral tracheal branches from the abdominal spiracles pass inwards, more or less parallel to one another, along the ventral surface of the body, and with the exception of the branch from the first and last of these spiracles, bifurcate to form a zig-zag **ventral longitudinal trachea** (*v. l.*) on each side of the median line as in the dorsal system, but in the former case this stout trachea only extends from the first to the last abdominal spiracles.

The ventral tracheal branch from the seventh abdominal spiracle does not bifurcate, the two lateral divisions of the ventral system not being connected at the posterior end, as is the case in the dorsal system.

Several small tracheæ are given off from the ventral longitudinal trachea of each side, and pass inwards to aerate the internal organs and ventral bands of longitudinal muscles.

A small trachea arises from the ventral branch near each spiracle.

The ventral branch from each of the prothoracic spiracles passes towards the median line, and both fuse to form a continuous, stout, transverse trachea (*t. t.*), which extends across the median line joining the two spiracles. Several smaller tracheal tubes arise from it, and aerate the muscles in the head and prothorax. A branch also passes into the first pair of legs.

The prothoracic spiracle is connected with the metathoracic spiracle by a small trachea (*c. tr.*), which arises near the former spiracle, and passing posteriorly, bifurcates, one branch passing into the second pair of legs, and the other joining the second tracheal trunk near the metathoracic spiracle.

The ventral tracheal branch from each of the metathoracic spiracles also fuse in the median line, and form a stout trachea, which lies transversely across the thorax, connecting the two spiracles, and giving off a number of smaller tracheæ, which aerate the muscles of the thorax. A small trachea arises from the tracheal trunk of this spiracle, and passes to the tracheal trunk of the first abdominal spiracle, giving off a branch to the third leg. A branch also passes forward into each of the second pair of legs.

D. The Circulatory System.

A tubular **heart** or **dorsal vessel** has been described by Witlaczil (1882, p. 35) as occurring in Aphis, and this author described its development in his later work (1884, p. 652).[1] Mordwilko (1895, p. 356) also refers to the presence of a chambered dorsal vessel in Trama. Dreyfus (1894, p. 238), on the other hand, was unable to find any trace of this structure in Phylloxera; and Grove (1909, p. 26) failed to find it in Siphonophora rosarum. I have been

[1] Ich fand bei Aphis dass das Herz und die Aorta aus einem Strang von Mesodermzellen gebildet werden, welcher Anfangs solid, durch Theilung seine zellen vermehrt und indem er sich aushölt, wahrscheinlich die Blutkörpchen enstehen lässt. Die venösen Ostien fand ich hier an der Grenze je zweier Segmente des Abdomens.

unable to establish its presence in the apterous viviparous female of S. lanigera.

E. The Reproductive System (Pl. 38, fig. 5; Pl. 41, fig. 35; Pl. 42, figs. 45, 46).

The **reproductive organs** of the apterous viviparous female occupy a considerable portion of the body. In general morphology they are simple in structure, and resemble in a general way those described by earlier investigators, such as Dufour (1833), Witlaczil (1882), etc., in other aphids.

They consist of a number of thin-walled tubes or large **ovarian cæca**, a pair of **oviducts**, and a stout, muscular **vagina** which leads to the **genital orifice**, the whole forming the **ovarium**.

The **ovarian cæca** (*p. c.*) are transversely constricted at intervals along their length, forming a series of several **ovarian chambers** (*p. a.*), in which the embryos are developed. The cæca are developed in two lateral groups of about five tubes in each group, and extend over the alimentary tract, throughout the body. In the posterior region of the abdomen they open into the two **oviducts** (*od.*), which pass beneath the rectum and unite in the region of the sixth abdominal segment to form the stout, muscular **vagina** (*v.*), which extends beneath the rectum to the **genital orifice** (*g. o.*).

The large ovarian chambers contain **embryos** in varying stages of development, those in the chambers nearer the genital orifice being more fully developed. In the earlier stages of development these embryos were called "pseudova." The development of the pseudovum has been described by Huxley (1858, p. 215) in an agamic stage of a species of Aphis. According to this author, it would appear that the embryos are developed from pseudova, which, surrounded by a vitelline substance, are set free in the chambers of the ovarian cæca, and eventually become changed into cellular germs, from which the germ-layers of the embryos are developed.

The terminal chambers of the cæca are small, and from the distal one is produced a fine thread-like **ovarian ligament.**

The **oviducts** are slightly flattened dorso-ventrally, and have stout muscular walls, with an inner epithelium of irregular, columnar cells bounding the duct.

The **vagina** is flattened dorso-ventrally, appearing narrow in longitudinal sections, but broad when viewed from the dorsal or ventral aspect. As seen in fresh preparations, it is whitish in colour, semi-transparent, and possesses stout, muscular walls.

The walls consist of a thick, outer layer of circular muscles, and a few scattered, inner, longitudinal muscles, with an epithelial layer of irregular cells, bordering the cavity (fig. 42).

As the vagina eaves the genital orifice it bends upwards, the muscular walls being thrown into folds.

The **genital orifice** is wide transversely, and is bounded by the genital and anal plates, which bear several stout bristly hairs.

The **embryos** are squeezed out through the orifice, posterior end first, by the muscular action of the vagina walls. As they emerge from the orifice they are smooth and glistening, the appendages adhering firmly to the sides of the body. The embryos are held by the head in the orifice for a few minutes after birth, and the anterior appendages are first set free from the sides of the body, the other legs being released soon afterwards.

F. The Muscular System.

The muscular system is well developed. For purposes of description the distribution of the various muscles may be conveniently treated as follows:

(1) The longitudinal body muscles. (2) The musculature of the head and its appendages. (3) The musculature of the thorax and ambulatory appendages. (4) The dorso-ventral muscles.

(1) The Longitudinal Body-muscles (Pl. 38, fig. 5;

Pl. 41, fig. 39).—These consist of four conspicuous bands of muscles lying along the ventral surface of the body, two on each side of the median line, and four beneath the dorsal integument. They are divided into two, three, or four bundles or fasciculi in each segment.

On the ventral surface the two **internal, ventral longitudinal bands** (*m. v'.*), lie one on each side of the median line, and extend from the antero-ventral border of the prothorax to the eighth abdominal segment.

The two **external, ventral bands** (*m. v.*) extend parallel to the lateral margins of the body. They reach from the antero-ventral border of the first abdominal segment to the eighth segment.

On the dorsal surface the two **internal, dorsal longitudinal bands** (*m. d'.*) extend from the eighth abdominal segment to the antero-dorsal border of the mesothorax, from which latter position each sends two diverging bands of muscles to the antero-dorsal border of the prothorax.

The **external, dorsal longitudinal muscles** (*m. d.*) extend from the antero-dorsal border of the metathorax to the eighth abdominal segment.

(2) The Muscles of the Head and its Appendages (Pls. 39 and 40).—(A) The **divaricator muscles of the pharynx** (*m. ph.*) are attached along the dorsal or anterior wall of the pharynx, and extend to the anterior wall of the clypeus. From the region of the pharynx protuberances, stout bands of lateral clypeal muscles (*m. p.*) pass outwards to become attached to the side walls of the clypeus.

(B) A few bands of **lateral muscles** (*m. f.*) extend across the lobes of the clypeus.

(C) Lying beneath the pharynx is the conspicuous **pump muscle** (*l. p. m.*), which is attached to the middle of the transverse bar and passes forwards beneath the pharynx, being inserted on the concave wall of the cylinder portion of the salivary pump (fig. 33). This muscle is divided longitudinally, and is spindle-shaped, being wider about the middle of its length.

Two small bands of muscles (*p. m.*) extend from the salivary pump to the ventral rods of chitin (*v. r.*).

(D) Two bands of **elevator muscles of the transverse bar** (*m. b′.*) extend from that structure in an antero-dorsal direction, to become inserted on the epicranial region of the head, and two similar bands of **depressor muscles** (*m. b.*) pass from this bar to the post-dorsal border of the head.

(E) Two bands of **depressor muscles of the head** (*m. h.*) are attached at its infra-posterior angles, and pass to the dorsal walls of the prothorax.

(F) The movements of the antennæ are controlled by a band of elevator (*m.* a^1.) and depressor (*m. a.*) muscles, which are attached to the antero-dorsal rods of chitin, near the ends of the transverse bar, and pass outwards to become inserted on the walls of the basal article of the antennæ.

(G) Two **elevator** and two **depressor muscles of the proboscis** (*m. pr.*) are inserted at the base of that structure and pass by the side of the thoracic ganglia to the dorsal wall of the thorax.

(H) The **retractor muscles of the mandibles** (*m′. m.*) are inserted on the internal face of the proximal ends of the mandibles, and pass through the head to become attached to the antero-dorsal rods of chitin of each side, near their origin from the transverse bar. The **protractor muscles** (*m.m.*) are attached to the antero-lateral walls of the frons, and pass upwards to become inserted along the base of the mandibular chitinous rods.

(I) The **retractor muscles of the maxillæ** (*m′. mx.*) are inserted at the proximal end of the maxillæ, and pass beneath the mandibular retractors to become attached to the antero-ventral rods of chitin, near the transverse bar.

The **protractor muscles** (*m. mx.*) are attached to the proximal ends of the maxillæ, and pass ventrally to the antero-ventral walls of the frons.

(3) The Musculature of the Ambulatory Appendages.—Two stout flexor muscles, which have their origin at the postero-dorsal margin of the mesothorax, are inserted on

the posterior face of the second pair of coxæ. Two similar flexor muscles extend from the post-dorsal margin of the metathorax to the third pair of coxæ.

A stout flexor and extensor muscle extend from the walls of each coxa to become inserted on the base of the trochanter.

A large extensor and a smaller flexor muscle extend throughout the femur. Inserted at the base of the tibia are a small flexor and extensor muscle, which continue throughout the article to the base of the tarsus.

(4) The Dorso-ventral Muscles of the Body.—Several bands of **dorso-ventral body muscles** extend from the floor of the thorax and abdomen to the dorsal and lateral walls of the body.

The **dorso-ventral muscles of the abdomen** (*m. v.*) arise from the ventral surface, close to, or a little external, to the outer longitudinal muscle bands, and pass upwards to become inserted on the dorso-lateral walls of the segments. It is these dorso-ventral muscles which bring about the respiratory movements of the body.

From the ventral surface of the seventh and eighth abdominal segments a band of muscles passes to each of the cornicles (*m. corn.*), and control the movements of the opening of those structures.

The Pseudo-vitellus.

Situated in the posterior half of the abdomen, lying by the side of, or between the ovarian cæca, are a few roundish conspicuous cells, which are usually joined together in groups of two or three cells, or in young females may form two larger masses (fig. 45, *pv.*).

When stained in sections with hæmatoxylin and eosin, the cytoplasm of these cells readily takes the eosin stain and appears to be quite granular. In the centre of the cell is a deeply staining nucleus with a nucleolus, but in some cells the nucleus is not seen.

These cells form the so-called pseudovitellus of Huxley and other authors, and the "Secundäre Dotter" described by Mecznikow (1866) in Coccidæ. Witlaczil (1882) has described them in Aphis, Krassilstschik (1892) in Phylloxera, Dreyfus (1894) in Phylloxera, Mordwilko (1895) in Trama, and Grove (1909) in Siphonophora; so that they appear to be generally present throughout the Aphididæ and probably the Coccidæ.

The origin and development of the pseudovitellus cells have been described by Will (1888) and also by Witlaczil (1884), but the function of these cells does not appear to be established. The appearance and distribution of them in the individual depends upon the stage of its development. In embryos of S. lanigera they form a conspicuous lobed mass of cells in the posterior region of the body. In mature, apterous viviparous females however, they degenerate into groups of two, three or more cells, lying to the side of the ovarian cæca in the posterior region of the body. I have observed in a few individuals, isolated pseudovitellus cells in the thoracic region of the body.

It would appear that these cells fulfil a nutritive function for the developing embryos, but Witlaczil (1882) considers them to be excretory in function.

Mordwilko (1895, p. 357) has briefly described the changes which take place in the pseudovitellus during the development of Trama. According to this author, the cells in young embryos of Trama form a tubular layer lying above the rectum, which, as the embryo develops, divides into three finger-like, longitudinal lobes, lying between the ovarian cæca. In mature adults only two cell masses are seen, which lie to the side of the body in the fifth and sixth segments, and these cells show signs of degeneration.

In addition to the pseudovitellus cells described above, there are in S. lanigera a few large cells situated in the posterior region of the body, which have a dirty-greyish, coarsely granular cell contents and a small nucleus (fig. 45, *y. c.*). When stained with hæmatoxylin and eosin they differ in appearance from the pseudovitellus cells, the cytoplasm being a dirty-yellowish colour, taking the eosin stain poorly and containing numerous dark coarse granules.

Scattered throughout the body cavity are a few isolated roundish cells which are smaller than the pseudovitellus cells, and are found in the head, thorax and abdomen, but chiefly in the head and thorax (fig. 22, *x*.). They have a greyish granular cytoplasm and a comparatively large nucleus, and resemble in appearance the cells described by Dreyfus (1894, p. 232, fig. 13, *x*.), in Phylloxera.

The Fat Body.

When examined in normal salt solution, the **fat body** is seen to consist of yellowish-brown masses of cells, which extend beneath the integument and over the internal organs. The cells are irregular in shape, much vacuolated, and possess numerous olive-coloured refractive granules and shining fat-globules.

As seen in sections, the fat body consists of several layers of cells, forming an irregular network beneath the integument and round the digestive tract. It is more extensively developed in the thorax and anterior segments of the abdomen, and is formed from the mesoblast cells lining the integument. In stained sections the cells of the fat body are seen to be irregular in shape with a much vacuolated cytoplasm and a small, irregular, stellate nucleus. The nucleus is surrounded by a layer of granular protoplasm and a similar layer extends round the periphery of the cell, strands of protoplasm passing across the cell between the two layers.

Bibliography.

Ashmead, W. H.—"A Generic Synopsis of the Aphidæ," 'Entomologica Americana,' vol. v, pp. 185–189 (1889).

Balbiani, E. G.—"Mem. sur la generation des Aphides," 'Ann. des Sc. Nat.,' tome xi, ser. 15, pp. 5–89 (1869).

Blomfield, J. E.—"Structure and Origin of Canker of the Apple Tree," 'Quart. Journ. Micr. Sci.,' vol. 50, pp. 573–579, 1 pl. (1906).

Brandt. E.—"Ueber das Nervensystem der Aphiden," 'Sitz. d. nat. Ges. Petersbourg,' Bd. vii (1876).

Buckton, G. B.—"A Monograph of British Aphides," Ray Soc., 4 vols. (1875–1882).

Bueno, J. R. de la Torre.—"On the Cornicles of Aphidæ" (chiefly an abstract of Horvath's paper), 'Canad. Entom.,' vol. xxxix, pp. 99, 100 (1907).

Bugnion, E., and Popoff, N.—"Les piéces buccales des Hémiptères," Ire. partie, 'Arch Zool. expér.' (5), tome vii, pp. 643–674, 3 pls., 8 figs. (1911).

Büsgen, M.—"Der Honigtau; Biol. Studien an Pflanzen u. Pflanzenlausen," 'Jena Zeitschr. f. Naturwiss.,' Bd. xxv, pp. 339–429 (1891).

Claus, C.—"Ueber die wachsbereitenden Hautdrüsen der Insekten." 'Sitzungsber. Gesells. z. Bedforderung d. Gesammt. Naturw. zu Marburg,' June, No. 8, pp. 65–72 (1867).

Dreyfus, L.—"Über Phylloxerinen," 'Abhandlung vorgelegt. der philos. Soc. Leipsig,' Wiesbaden (1889).

——— "Zum Kapitel der Hautungen," 'Zool. Anzeig.,' Bd. xiv, p. 61 (1891).

——— "Zu J. Krassilstschik's Mittheilungen über die Vergleichende Anat. u. Systematik der Phytopthires mit besonders Bezugnahme auf die Phylloxeriden," 'Zool. Anz.,' Bd. xvii, pp. 205–208, 221–235, 237–242, 2 pls. (1894).

Dufour, M. Léon.—"Recherches anatom. et physiol. sur les Hémiptères," 'Mem. pres. a l'instit. de France,' Tome iv, Aphidiens, pp. 241–245, 359, 369, 387, 418, figs. 114–117, and 192 (1833).

Flögel, J. H. L.—"Monographie der Johannisbeern Blattlaus (Aphis ribis, Linn.)," 'Allg. Zeitschr. fur Entom.,' Bd. ix, pp. 321–333, 375–382 (1904).

——— "Monographie der Johannisbeern Blattlaus (Aphis ribis, Linn.)," continuation and conclusion, 'Zeitschr. Insbiol.,' Bd. i, pp. 49–63, 97–106, 145–155, 209–215, 233–237 (1905).

French, C.—'Handbook of Destructive Insects of Victoria,' part i, p. 37 (1904).

Froggatt, W.—"Woolly Aphis or American Blight," 'Agric. Gaz. N. S. Wales,' vol. xiv, pp. 18–25, 1 fig. (1903).

Gillette, C. P.—"Honey Dew and the Cornicles of Aphidæ," 'Canad. Entom.,' vol. xl, pp. 235, 236, 1 fig. (1908).

Goethe, R.—"Die Bekämpfung der Blutlaus," 'Mitteilungen über obst. und Gartenbau,' Jahr. 1898, Nr. 12, and 1899, Nos. 1 and 3 (1898).

——— "Die Blutlaus, Schizoneura lanigera, Hausm. Ihre Lebengeschichte und Bekämpfung," 'Verlag. fur Landwirtschaft, Gartenbau,' etc., Berlin (1909).

Grove, A. J.—"The Anatomy of Siphonophora rosarum, Walk," part i, 'Journ. of Parasitology,' vol. ii, No. 1, pp. 1–28, 1 pl., 15 text-figs. (1909).

Horvath, Dr. G.—"Sur les Cornicles ou Nectaires des Aphidiens," 'C.R. 6me. Congres. Intern. de Zool. Sceance,' 1904, pp. 422–424 (1904).

Huxley, T. H.—"On the Agamic Reproduction and Morphology of Aphis," parts i and ii, 'Trans. Linn. Soc.,' vol. xxii, pp. 193–219, 221–236, pls. 36–40 (1857–1858).

Kaltenbach, J. H.—"Monographie der Familien der Pflanzenläuse" (1843).

Kershaw, J C.—"Notes on the Salivary Glands and Syringe of two Species of Hemiptera" (Pristhesancus papuensis, Stäl.: Enectus elongatus Dist.), 'Ann. Soc. Entom. Belgique,' tome lv, pp. 80–83, 4 figs. (1911).

Kowalevsky, A.—"Ein Beitrag zur Kenntnis der Exkretionsorgane," 'Biol. Centralb.,' Bd. ix, Nr. 2, Insekten, pp. 42–47 (1889).

Krassilstschik, von J.—"Zur Vergleichenden Anatomie und Systematik der Phytophthires," 'Zool. Anz.,' Bd. xvi, pp. 85–92, 97–102 (1893A).

——— "Zur Anat. und Histol. der Phylloxera vastatrix, Planchon," 'Horæ Societatis entomologicæ Rossicæ,' tome xxvii, pp. 1–37, taf. i, ii (1893B).

Künckel, J.—"Recherches sur les Organes de Secretion chez les Insectes," 'Ann. Soc. Entom. France,' tome vii, ser. 4, pp. 43–46 (1867).

Lemoine, M. Victor.—"Sur le Systeme Nerveux du Phylloxera," 'Comp. Rend.,' tome ci, pp. 961–963 (1885).

Lohrenz, H. W.—"The Woolly Aphis—Schizoneura lanigera," 'Journ. Econom. Entom.,' vol. iv, pp. 162–170, 1 pl. (1911).

Mark, E. L.—"Beiträge zur Anat. und Hist. der Pflanzenläuse insbesondere der Cocciden," 'Archiv. f. mikroskop. Anat.,' Bd. xiii, pp. 31–86, taf. iv–vi (1887).

Marlatt, C. L.—"The Hemipterous Mouth," 'Proc. Entom. Soc. Washington,' vol. iii, no. 4, pp. 241–249, 3 figs. (1895).

Marlatt, C. L.—"The Woolly Aphis of the Apple, Schizoneura lanigera, Hausm.," 'U. S. Dept. Div. Entom. Circ.,' No. 20, 2nd ser., 7 figs. (1897).

Mayer, P.—"Zur Anatomie von Pyrrhocoris apterus," 'Arch. f. Anat. und Physiol.,' pp. 313–347 (1874); pp. 309–355 (1875), taf. vii–ix; ix, x (1874–5).

Mecznikow, El.—"Embry. Studien an Insecten," 'Zeitschr. f. wiss. Zool.,' Bd. xvi, pp. 389–500 ('Die Entwick. der vivip. Aphiden,' pp. 437–459), (1866).

Mordwilko, A. von.—"Zur Anat. der Pflanzenläuse Aphiden," Gattungen, Trama (Heyden), Lachnus (Illiger), 'Zool. Anz.,' Bd. xviii, pp. 345–364, figs. 1–10 (1895).

——— "Tableaux pour servir a la determination des Groupes et des Generes des Aphidæ" (in Russian), 'Ann. du Mus. Zool. de l'Acad. Imp. d. Sciences de St. Petersbourg,' tome xiii (1908).

Nietsch, Vicktor.—"Die Mundtheile der Rhynchoten," 'Mitt. nat. ver. Steirmark,' Bd. xliv, pp. 304–311 (1908).

Oestlund, O. W.—"Antennal Sense-Organs of Aphidæ," 'Bull. Minnesota, Acad. Nat. Sc.,' vol. iv, pp. 219, 220 (1906).

Passerini, J.—"Aphididæ italicæ," 'Archivio, per la Zool. l'Anat., etc.,' vol. ii, fasc. 2, pp. 129–208 (1863).

Packard, A. S.—'A Text-Book of Entomology' (1903).

Riley, C. V.—"The Nervous System and Salivary Glands of Phylloxera," 'Psyche,' 1879, vol. ii, No. 60, pp. 225–226 (1879).

Rumsey, W. E.—"Manner of Birth of Woolly Aphis of Apple (Schizoneura lanigera) and other Aphidæ," 'U. S. Dept. Agric. Div. Entom. Bull.,' No. 67, pp. 31–34 (1907).

Sharp, D.—'Camb. Nat. Hist.,' vol. vi, "Insects," part ii, pp. 532–544, 581–591 (1899).

Schneider, A.—"Ueber den Darmkanal der Arthropoden," 'Zool. Beiträge,' Bd. ii, pp. 81–96 (1890).

Smith, J. B.—"An Essay on the Development of the Mouth Parts of Certain Insects," 'Trans. Amer. Philos. Soc.' (read February, 1896), vol. xix, new series, pp. 175–198, 3 pls. (1898).

——— "The Structure of the Hemipterous Mouth Parts," 'Science,' April, 1892, pp. 189, 190, figs. 1–5 (1892).

Sorby, H. C.—"On the Colouring Matter of Some Aphides," 'Quart. Journ. Micr. Sci.' vol. xi, pp. 352–361 (1871).

Theobald, F. V.—" Woolly Aphis or American Blight, and a Related Subterranean Species," 'Journ. S. East. Agric. Coll.,' No. 6, pp. 15–21 (1897).

——— 'Insect Pests of Fruit,' pp. 141–153 (1909).

Tullgren, A.—" Aphidologische Studien," part i, 'Arkiv. för Zoologi,' Bd. v, No. 14, pp. 1–190, 92 text-figs. (Schizoneura, p. 161) (1909).

Vickery, R. A.—" A Comparative Study of the External Anatomy of Plant Lice," '12th Rept. State Entom. Minnesota,' p. 178 (1908).

Wedde, Hermann.—" Beiträge zur Kenntnis des Rhynchotenrüssels," 'Arch. f. Naturgesch.,' li, Bd. i, pp. 113–143, 2 taf. (1885).

Witlaczil, E.—" Zur Anatomie der Aphiden," 'Arb. Zool. Inst. Univ. Wien.,' Bd. iv, pp. 397–441, 3 taf. (1882A).

——— " Zur Anatomie der Aphiden," 'Zool. Anzeig.,' Bd. v, pp. 239–241 (1882B).

——— " Entwicklungeschichte der Aphiden," 'Zeit. für wiss. Zool.,' Bd. xl, pp. 559–696, 9 taf. (1884).

Will, L.—" Entwicklungeschichte der viviparen Aphiden," 'Spengel's Zool. Jahrbucker, Abth. d. Anat. u. Ontogenie der Thiere,' Bd. iii, pp. 201–286, taf. i—x (1888).

EXPLANATIONS OF PLATES 38–42,

Illustrating Mr. J. Davidson's paper on "The Structure and Biology of S c h i z o n e u r a l a n i g e r a, Hausmann or Woolly Aphis of the Apple Tree.—Part I: The Apterous Viviparous Female."

Reference Lettering.

a. Antenna. *a d.* Antero-dorsal rod. *ab. i-ix.* Abdominal segments. *a. f.* Articulation of clypeus with epicranium. *a. g.* Abdominal ganglion. *an.* Anus. *ap.* Anal plate. *a. s.* 1–7. Abdominal spiracles. *a. t.* Anterior dorsal trachea. *a. v.* Antero-ventral rod. *b. c.* Buccal cavity. *b. i.* Body integument. *b. ta.* Basal joint of tarsus. *c.* Chitinous thickening at posterior end of buccal cavity. *cd.* Cylinder or " Kolben " of salivary pump. *c. i.* Integumental lip over opening of cornicle. *cl.* Claws. *cn.* Cornicle. *c. o.* Opening of cornicle. *cox.* Coxa. *cs.* Commissure. *c. t.* Connective tissue. *c. tr.* Stout trachea connecting thoracic spiracles. *cy.* Cytoplasm. *d. b.* Dorsal tracheal branch. *d. f.* Dorsal wall of clypeus. *d. h.* Dorsal wall of head. *d. t.* Dorsal longitudinal trachea. *e.* Embryos. *e. c.* Epithelial cells. *e. s.* Epithelial cells of stomach. *f. a.* Integumental areas of wax-glands. *fac.* Facets of the eyes. *f. b.* Fat body. *fe.* Femur. *fr.* Clypeus. *g.* Ganglion. *g. c.* Ganglion cells. *g. o.* Genital orifice. *g. p.* Genital plate. *g. s.* Granules of secretion. *h.* Hypopharynx. *hd.* Head. *hr.* Integumental hairs. *hs.* Hypodermis. *i.* Intestine. *i. h.* Infra-posterior wall of head. *in.* Intima. *lbr.* Labrum. *l. g.* Longitudinal proboscis groove. *lr. g.* Longitudinal groove on labrum. *l. t.* Ligament of connective tissue. *lu.* Lumen. *lu. s.* Lumen of stomach. *m.* Large pump muscle. *m. a.* Depressor muscles of antenna. *m. a'.* Elevator muscles of antennæ. *m. b.* Depressor muscles of transverse bar. *m. b'.* Elevator muscles of transverse bar. *m. c.* Circular muscles. *m. cn.* Muscles controlling cornicles. *m. cox.* Coxal muscles. *m. d.* External dorsal longitudinal muscles. *m. d'.* Internal dorsal longitudinal muscles. *m. f.* Lateral muscle of clypeus. *m. g.* Mid-gut. *m. h.* Depressor muscles of head. *m. l.* Longitudinal muscles. *m. m.* Protractor muscles of mandibular setæ. *m'. m.* Retractor muscles of mandibular setæ. *m. mx.* Protractor muscles of maxillary setæ. *m'. mx.* Retractor muscles of maxillary setæ. *m. p.* Lateral divaricator muscles to the wall of clypeus. *m. ph.* Divaricator muscles of pharynx. *m. pr.* Proboscis muscles. *m. r.* Mandibular chitinous rods. *m. s.* Metathoracic spiracle. *m. t.* Dorso-ventral muscles of thorax. *m. v.* External ventral longitudinal muscles. *m. v'.* Internal ventral longitudinal muscles. *m. v. d.* Dorso-ventral muscles. *ma.* Metathorax. *ma. g.* Metathoracic ganglion. *md.* Mandibular setæ. *md. o.* Mandibular organs. *mo.* Mesothorax. *mo. g.* Mesothoracic ganglion. *mx.* Maxillary setæ. *mx. o.* Maxillary organs. *mx. r.* Maxillary chitinous rods. *n.* Nucleus. *no.* Nucleolus. *n. a.* Antennal nerve. *n. l.* 1–3. Leg nerves. *n. m.* Nerve to muscles. *o.* Outer wall of œsophageal valve. *œs.* Œsophagus. *oc.* The eyes. *oc. n.* Nerve to eyes. *od.* Oviducts. *om.* Pigment. *p.* Post-abdominal nerve. *p. a.* Ovarian chambers *p. c.* Ovarian cæca. *p. g.* Post-abdominal ganglion. *ph.* Pharynx. *p. m.* Pump muscles attached to *v. r.* *po.* Prothorax. *p. p.* Pharynx protuberances. *pr.* Proboscis. *p. s.* Prothoracic spiracle. *pv.* Pseudovitellus cells. *r.* Rectum. *r. o.* Retort-shaped organs of embryo. *s.* Salivary pump. *s. a.* Anterior salivary gland. *sb. g.* Sub-œsophageal ganglion. *s. c.* Salivary pump chamber. *s. d.* Salivary duct. *s. g.* Supra-œsophageal ganglion. *s. o.* Antennal sense-organs. *s. p.* Posterior salivary gland. *s. p.* Spiracle. *s. r.* Main trachea from spiracle. *st.* Stomach. *seg. n.* 1, 2. Segmental nerves from *p.* *t.* Tactile hairs. *ta.* Tarsus. *t. g.* Thoracic ganglion. *ti.* Tibia. *tr.* Trachea. *tro.* Trochanter. *t. t.* Thoracic trachea joining the spiracles. *v.* Vagina. *v. b.* Ventral tracheal branch. *v. l.* Ventral longitudinal trachea. *v. r.* Ventral chitinous rods. *w.* Wall of the ovarian chamber. *w. c.* Wax-gland cells. *w. f.* Wall of clypeus. *w. gl.* Wax-gland. *w. h.* Wall of head. *w. s.* Wax-sac. *w. s′.* Solidified contents of wax-sac. *x.* Cells described in text. *y. c.* Large cells with coarse granular contents.

PLATE 38.

Fig. 1.—Apterous viviparous ♀, ventral. × 45.

Fig. 2.—Apterous viviparous ♀, dorsal. × 45. 2 B. Wax-glands showing integumental facettes. 2 C. Eyes showing tubercles.

Fig. 3.—Head, anterior portion (frons), showing endoskeleton as seen from dorsal or anterior aspect. × 375.

Fig. 4.—Appendages: (A) Leg 1; (B) leg 2; (C) leg 3. × 85. (D) antenna (right) ventral side. × 110.

Fig. 5.—Apterous viviparous ♀, dissection from dorsal surface showing distribution of internal organs; the dorsal integument, dorsal longitudinal muscles and tracheal system removed. × 85.

PLATE 39.

Figs. 6–21.—Series of transverse sections through the head, being at right angles to its longer axis, showing relationship of endoskeleton, pharynx, buccal appendages and musculature. × 250.

Fig. 22.—Longitudinal section through side of the head. × 135.

Fig. 23.—Longitudinal section through head, passing through the end of the transverse bar. × 135.

Fig. 24.—Longitudinal section through head and thorax, almost median. × 235.

PLATE 40.

Figs. 25–32.—Series of vertical sections through head, showing relation of parts of endoskeleton, buccal appendages and musculature. × 200.

Fig. 33.—Vertical section through head showing salivary pump, etc. × 375.

Fig. 34.—Transverse section through thorax showing retracted proboscis. × 200.

PLATE 41.

Fig. 35.—Apterous viviparous ♀, internal organs from right side, slightly schematised. Drawing made from dissections and serial sections. × 100.

Fig. 36.—Nervous system and salivary glands, dissection from ventral surface. × 110.

Fig. 37.—Transverse section through the rectum; hæmatoxylin (Ehrlich) and eosin. × 710.

Fig. 38.—Transverse section through small intestine; hæmatoxylin (Ehrlich) and eosin. × 710.

Fig. 39.—Apterous viviparous ♀, dorsal, showing dorsal longitudinal muscles and dorsal tracheal system. × 68.

Fig. 40.—Transverse section through stomach in region of œsophageal valve; hæmatoxylin and eosin. × 710.

Fig. 41.—Longitudinal section through salivary glands; hæmatoxylin and eosin. × 780.

Fig. 42.—Transverse section through the vagina; hæmatoxylin and eosin. × 710.

PLATE 42.

Figs. 43–46.—Transverse sections through the body; hæmatoxylin and eosin. × 135.

Fig. 43.—Transverse section through region of anterior salivary glands.

Fig. 44.—Transverse section through region of posterior salivary glands, showing salivary duct passing beneath the ganglion.

Fig. 45.—Transverse section through anterior segment of abdomen.

Fig. 46.—Transverse section through region of cornicles.

Fig. 47.—Section through the unicellular wax-glands; hæmatoxylin and eosin. × 1100.

Fig. 48.—Longitudinal section through the stomach and œsophageal valve; hæmatoxylin and eosin. × 780.

Fig. 49.—Section through one of the lateral eyes; stained hæmatoxylin and eosin. × 780. The hypodermis has shrunk away from the chitin.

Appendix.

Through the kindness of Mr. Clifford Dobell my attention has been directed to the recent works of Dr. Karel Šulc and Dr. Paul Buchner on the pseudovitellus in Hemiptera. I regret that owing to the fact that the manuscript had already gone to press, I am unable to incorporate the work of these authors in the text.

Šulc, Dr. Karel.—"'Pseudovitellus' und ähnliche Gewebe der Homopteren sind wohnstätten symbiotischer Saccharomyceten," 'Separatabdruck aus den Sitzungsberichten der Königl. Böhm. Gesellschaft der Wissenschaften in Prag,' 1910, pp. 1–39, 18 text-figs. (1910).

Buchner, Dr. Paul.—"Studien an intracellularen Symbionten: I, Die intracellularen Symbionten der Hemipteren," 'Archiv. f. Protistenkunde,' Bd. xxvi, pp. 1–116, Taf. 1–12, and 29 text-figs. (1912).